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Title:

Ecology of charophytes – permanent pioneers and ecosystem engineers

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Abstract

For almost a century, charophytes have been regarded as a group that is confined to low-nutrient-clear water conditions. In light of recent research, this generalisation of the ecological niche dimensions of charophytes has changed and now includes more facets of ecological existence. In this review, the current knowledge with respect to species-specificity as well as temporal aspects – ontogenetic and successional ones – of the ecological requirements of charophytes are presented and discussed. This review identifies new directions for ecological research on charophytes as well as knowledge gaps to be filled, not just for reasons of academic curiosity, but also for applied purposes such as lake restoration, bioremediation and bioindication of water quality and water regime.

Introduction

Charophytes are morphologically complex green algae, belonging to the Streptophyta. They display differentiation into rooting structures (rhizoids) and photosynthetic structures (axes, branchlets, bract-cells), and they have multicellular reproductive organs (oosporangia and antheridia) (Figure 1). They are among the closest relatives of the first land plants (Karol et al. 2001), and have been used as model organisms for studying the physiological aspects of terrestrial acclimation, salinity tolerance and membrane processes (Braun et al. 2007; Beilby and Casanova 2014). Charophytes are also important bioindicators of water quality and water regime (for review see Doege et. al 2016); and their capacity to absorb pollutants from freshwater makes them useful for bioremediation (Kalin et al. 2002a, 2002b; Marquardt and Schubert 2009). Concerns about the declining state of water resources has led to intensive study of both these aspects over the few last decades. The use of charophytes for bioindication has become a common tool for environmental monitoring (e.g. Gutowski et al. 1998; Kohler 1982; Krause 1981; Melzer 1994; Van Raam 1998; Burns et al. 1999; Jäger 2000; Selig et al. 2009).

Most of the bioindication protocols have a focus on water quality, in particular, nutrient availability. This is based on the observation that charophytes can be a key element of aquatic ecosystems, able to create and maintain clear-water conditions by a network of biological interactions (van den Berg et al. 1998a; Blindow et al. 2002; Casanova et al. 2002; Meurer and Bueno 2012).

However, the bioindication protocols that have been developed tend to be region-specific (Doege et al. 2016). Intercalibration between „regional schemes“ is possible, but complicated (Schneider 2007), not only because of the problematic taxonomy in family Characeae, but in relation to data management (Doege et al. 2016). This is highlighted by the fact that some species that are considered to be rare and threatened in their native area have successfully spread to other regions (Karol et al. 2017) raising serious questions about their effective ecological niche dimensions (Alix et al. 2017).

Previous reviews have focused on charophyte distribution in relation to water chemistry (nutrients, salinity) and physical properties (pH, temperature, e.g. Corillion 1957; García and Chivas 2006; Rey-Boissezon and Auderset Joye 2015). In this review, the authors will present a more holistic approach to charophyte ecology,

including aspects of biological interactions as well as their occurrence in relation to sediment properties, the availability of diaspores and phenology.

For this, all stages in the charophyte life cycle from the dispersal and germination of viable oospores, through requirements for establishment and growth, interactions with the biotic and abiotic environment, to the formation of a sustainable diaspore reservoir (oospores and vegetative propagules: bulbils) will be reviewed.

Arriving at the new town: distribution pathways of charophytes

Charophytes occur on every continent. In contrast to former statements, this includes Antarctica based on a *Nitella* sp. specimen collected by T.E. Berg in 1964 at Marble Point, which is close to the McMurdo station, deposited in Leiden (#64010201 of the Zaneveld-collection).

Charophytes prefer freshwater or brackish water habitats rather than open marine situations, and can be found in a wide variety of standing and slow-moving waters (Martin et al. 2003). Some species are widespread (e.g. *Nitella hyalina* (DC.) C. Agardh 1824, *Chara zeylanica* Willd. 1805, *Chara globularis* Thuill. 1799), but many charophytes have a limited geographical distribution. Charophytes are usually the first macrophytes to arrive in newly created ponds and lakes, leading to some species being described as „permanent pioneers“ (Krause and Walter 1985).

Anthropogenic dispersal pathways exist e.g. via recreational fishing, shipping, bathing and diving (Karol and Sleith 2017), but there are two important non-anthropogenic processes that can explain in part, the success of charophytes in rapid colonisation, recolonization and long-distance dispersal via oospores (spatial as well as temporal dispersal) and via bulbils (preferentially temporal dispersal). Charophyte oospores range in size from ~180 to >>1000 µm (Wood 1959; Haas 1994; Krause 1997) and are an agent of long- and short-distance dispersal to different wetlands. Bulbils (vegetative propagules) are thought to be important for local persistence (Van den Berg et al. 2001; Bonis and Grillas 2002; Brochet et al. 2010) and dispersal within water bodies, but as they are not resistant to desiccation, they are less likely to be successfully dispersed to different, or newly created habitats.

Where there is variation in the production of oospores by individual charophyte species, it is likely that those that produce copious amounts of oospores will be

widely dispersed and locally persistent (Baastrup-Spohr et al. 2015). Within lakes or wetlands, wind can play an important role in dispersal via wind-induced currents (Soomers et al. 2010). Also, charophyte oospores are very light, and wind dispersal could be significant when wetlands dry (Bakker et al. 2013). There is a body of evidence supporting the role of water birds as principal agents of long-distance dispersal (Olsen 1944; Proctor 1959, 1962). In studies on the dispersal of propagules of aquatic macrophytes (Green et al. 2002: Charalambidou and Santamaria 2005; Brochet et al. 2010; Figuerola et al. 2010; Pollux 2011) smaller-sized propagules are more likely than large propagules to survive gut passage in birds, and germinate afterwards (Soons et al. 2008). Because of the lack of organs for attachment, oospores are more likely to be transported internally in the birds alimentary tracts than externally. *Chara* spp. have even been found to have enhanced germination after passage through the gut (Brochet et al. 2010; Figuerola et al. 2010). However, as Proctor (1980) pointed out, although water birds can readily distribute charophyte oospores, not all species occur everywhere and there are numerous examples of short-range endemism.

Species of *Chara* display a divergent biogeographic pattern (Proctor 1980), i.e. some species are restricted to a single continental area whereas others are distributed across large, supracontinental areas or are close to cosmopolitan. Proctor (1980) hypothesised that the sexual reproductive system of charophytes had an impact on biogeography, contending that cosmopolitan *Chara* species are monoecious (male and female gametangia on the same plant), whereas dioecious species (separate male and female plants), are confined to smaller areas. Dioecious species depend on the arrival of more than one oospore, whereas monoecious species can, in theory, establish a population from a single oospore. To date this conjecture has been supported by all new discoveries of dioecious charophytes (e.g. García and Casanova 2003; Casanova 2014). However, irrespective of being broadly accepted, the evidential support might not be as strong as expected. Where the genetic identity of individual taxa has been confirmed, only a few taxa are found on more than one continent for both monoecious as well as dioecious species. Of course, it is striking that the only charophyte species that is able to reproduce parthenogenetically, the dioecious *Chara canescens*, is found all over Europe and even in the Southern Hemisphere in its apomictic form (Casanova and Nicol 2009, Schaible et al. 2012), whereas sexually reproducing dioecious populations are very rare (Schaible et al.

2009, 2011). On the other hand Proctor (1971) demonstrated reduced interfertility between individuals of cosmopolitan (monoecious) species, originating from different continents. Consequently, Proctor's hypothesis (Proctor 1980) should be critically re-examined in the light of the increasing distribution data available.

Establishing stands: breaking dormancy and induction of germination

Charophytes have three options to establish stands: A) vegetative growth from omnipotent nodal cells (Skurzyński and Bociąg 2011), B) vegetative growth from bulbils (Asaeda et al. 2007; Wang et al. 2015) or, C) germination of sexually produced oospores. Charophytes exhibit apical dominance, so lower nodal cells are activated „automatically" when the apical cell is removed or damaged (Schubert et al. 2016; Kuczewski 1906; Pringsheim 1863). Bulbils – irrespective of their origin – are omnipotent cells too, but they contain starch storage cells, which enhances the capacity to endure periods of unsuitable conditions and improves the competitive ability of the vegetative offspring. Bulbil formation has been studied intensively by Giesenhagen (1896). However, the mechanisms for activation of bulbil complexes as well as induction of bulbil formation have been little studied (c.f. Casanova 1994). In laboratory incubation, bulbils usually germinate instantaneously and do not require pretreatments to achieve high germination rates (Steinhardt and Selig 2011; Nowak et al. 2017). This raises the question of how germination of bulbils is suppressed under natural conditions, preventing germination before the death of, or release from, the parent plant (Giesenhagen 1896).

The regenerative options for charophytes (basal growth, bulbil activation and oospore germination) vary temporally. Nodal cells allow for immediate replacement of damaged axes, whereas bulbils allow limited growth even if nutrient and light availability is poor, and may survive short periods of unsuitable conditions, e.g. winter periods (Giesenhagen 1896; van den Berg et al. 2001).

Oospores allow for an even longer temporal response: they are protected by a multi-layered oospore wall (Leitch et al. 1990) from chemical and physical hazards, and contain a significant storage of starch for protonemal growth. They display a high degree of primary and secondary dormancy so that even if conditions are suitable for germination only a small proportion of the available pool of oospores, in contrast to

bulbils, germinate at any one time (Casanova and Brock 1990, 1996; Vleeshouwers et al. 1995; van den Berg et al. 2001; Asaeda et al. 2007; Wang et al. 2008). Primary dormancy has been related to the concentration of abscisic acid (Sabbatini et al. 1987; Sederias & Coleman 2007; Penfield & King 2009). After the period of primary dormancy, the oospore becomes susceptible to triggers that induce germination. Hilhorst (1993) developed a physiological model of dormancy, which has been shown to be applicable for charophytes as well (Holzhausen et al. 2017). Oospores can enter into a secondary dormancy if the germination 'window' is not available in any one year (Sokal and Stross 1986). Studies have shown that oospores can survive in seed banks for at least 10 years, and sometimes more than 40 years (Rodrigo et al. 2010). As such oospores can be maintained in lakes and wetlands as a long-lived, dormant bank of propagules that is rarely totally depleted (van den Berg et al. 2001).

Low temperatures (e.g. Forsberg 1965; Casanova and Brock 1996) as well as osmotic shock (e.g. Proctor 1967; Casanova and Brock 1996; Lambert 2013; Lambert et al. 2013) can stimulate germination via synthesis of gibberellins (Hilhorst 1993; Vleeshouwers et al. 1995; Penfield and King 2009) when irradiance conditions are favourable (Sabbatini et al. 1987; van den Berg et al. 1998a; Matheson et al. 2005; Kalin and Smith 2007; Sederias and Coleman 2007; 2009).

The specific conditions required for breaking dormancy and induction of germination, differ among species (for a detailed discussion see: Holzhausen et al. 2017). Temperature, drying, osmotic conditions and redox conditions as well as irradiance required for activation of oospores are related to the ecological conditions and seasonality the species prefer (Forsberg 1965; Bonis and Lepart 1994; Casanova and Brock 1996). Exposure to light can be required for some species, and is vital for successful establishment (de Winton et al. 2004). Seasonality (Sokol and Stross 1986) can play an important role for some species, whereas others are insensitive to some of the factors dealt with in Hilhorst's (1993) model (see, e.g. Shen 1966; de Winton et al. 2004).

Growing to fertility – abiotic requirements for a happy charophyte life

Most studies on the growth conditions for charophytes concentrate on easily measured physical and chemical characteristics of water bodies, such as light, nutrients, pH and conductivity. These have been considered to be the most important determinants of charophyte distribution and diversity, both within and among aquatic

environments (van den Berg et al. 1998a, Blindow et al. 2014). For some of these hydrological characteristics there are clear limits or tolerances that can be tabulated for individual charophyte species (e.g. Corillion 1957, García and Chivas 2006; Rey-Boissezon and Auderset Joye 2015). As a consequence of this apparent sensitivity, particularly to nutrient status, the occurrence of charophytes has widely been applied as an indicator of low trophic level in waterbodies (Krause 1981; Schwarz and Hawes 1997; Melzer 1994; Schneider 2007; Doege et al. 2016). However, there are likely to be interactions among the physical and chemical characteristics of water (e.g. light reduction from biological turbidity resulting from eutrophic conditions), as well as variation in charophyte responses in relation to less frequently measured sediment characters, depth, temperature, wave action and water-level fluctuations.

Charophytes can take up nutrients through their photosynthetic thalli as well as through the rhizoids. They can accumulate nitrogen, primarily as ammonium-N, and phosphates (Beilby and Casanova 2014). In general, charophytes are dominant constituents of submerged plant communities at low nutrient concentrations, where they can form extensive underwater meadows (“beds”). As nutrient concentrations increase charophyte dominance declines and angiosperm abundance increases. Under high nutrient conditions charophytes can completely disappear. This sensitivity to eutrophication was initially explained as a toxic effect from phosphorus (Forsberg 1965), however later studies showed that *Chara* species could maintain high growth rates at elevated phosphorus concentrations when light is not limiting (Henricsson 1976, Blindow 1988). In fact, a number of charophytes can be found at total phosphorus concentrations exceeding 0.4-0.5 mgl^{-1} e.g. *Nitellopsis obtusa* (Doege et al. 2016). Mean values of total phosphorus, however, are often lower than 0.1 mgl^{-1} in charophyte sites. In high nutrient waters, charophytes are restricted to shallow sites where light is not a limiting factor (Blindow 1992).

Charophytes have evolved mechanisms to maximize efficient use of light even under unfavorable conditions. They are able to exist with as little as 1.5% of the light that reaches the surface of the water (Schwarz et al. 1999). Consequently, charophytes can be found in oligotrophic lakes down to as much as 65 m (Kufel and Kufel 2002), and in shallow turbid water where the Secchi depth is less than 5 cm (Casanova and Porter 2013). Light use efficiency allows also persistence during the winter with thick ice cover (Pukacz et al. 2016a; Pełechaty et al. 2017). Some charophyte species experience shading as a result of mineral encrustation directly on the surface of thalli

(Raven et al. 1986; Martin et al. 2003) as well as within dense conspecific communities. Conversely some charophyte species in shallow waters need protection from high light intensity and UV-B radiation. These species can produce high concentrations of carotenoids, which protect the plants (in particular antheridia) from excessive light intensity (Wang et al. 2015).

In stable conditions charophytes have a high degree of morphological plasticity that allows responses to changing light conditions. Similar to embryophytes, the effects of light attenuation in the water column, along with depth, increase morphological variability (Blindow and Schütte 2007; Pukacz et al. 2014; Schneider et al. 2015) and variability in biomass production (Pełechaty et al. 2013; Pukacz et al. 2016a).

Not all species react equally to worsening light conditions. Species with large thalli (> 1 mm internode diameter) are the first to decline, whereas the smaller ones (< 1 mm internode diameter) can still survive in the shallow sites (Blindow 1992). Some species with large thalli (e.g. *Chara aculeolata* Kütz. in Rchb. 1832 and *Chara tomentosa* L. 1753) can “move” to the shallow sites when they have sufficient morphological plasticity (e.g. Krause 1997; Urbaniak and Gąbka 2014). Similarly, there are species that only persist as scattered individuals in shallow water, which never form extensive “beds” (Casanova and Brock 1999). For those species wave action, sediment type, water regime and biological interactions are likely to be major influences on their distribution and abundance.

Classical studies show that charophytes prefer calcium rich, hard and alkaline waters. In fact, the pH tolerance is generally wide and differs among taxa. While *Chara*, *Nitellopsis*, *Tolypella* and *Lychnothamnus* usually occur in alkaline environments with mean pH values between 6.0 to 9.0, *Nitella* species tend to occur in slightly acidic to neutral soft waters (as summarized in Martin et al. 2003 and Doege et al. 2016). Water hardness and alkalinity are linked to bicarbonate (HCO_3^-) concentrations in waters as a result of $Ca(HCO_3)_2$ dissociation and the CO_2 – HCO_3^- equilibrium. Water pH directly affects the degree of dissociation and the proportions of CO_2, HCO_3^- and CO_3^{2-} ions so that bicarbonates are dominant in alkaline waters (Wetzel 2001). The primary mechanism of carbon assimilation in charophytes is the conversion of bicarbonates into CO_2 that diffuses into the charophyte cell, additionally resulting in $CaCO_3$ precipitation onto the surface of the charophyte thallus (Raven et al. 1986). This results in the characteristic populations of heavily encrusted

charophytes in Ca-rich freshwaters, where these macroalgae contribute to the calcite precipitation and storage in bottom sediments (as summarized in Pełechaty et al. 2013). Calcite precipitation could have a significant ecological consequence if there is co-precipitation of phosphorus from the water column, allowing charophyte beds to act as nutrient sinks (Kufel and Kufel 2002). In addition, biomineralization results in decalcification of the water (Pukacz et al. 2013).

Many charophyte species tolerate brackish to saline water. In the highly variable brackish water environment charophytes require the capacity to regulate osmotic processes and ion concentrations. Salinity-tolerant charophytes regulate their turgor pressure in response to osmotic pressure change of the medium based on the accumulation of Na^+, K^+ and Cl^- ions and sucrose. In contrast, obligate freshwater charophytes do not regulate their turgor pressure, but adjust internal osmotic pressure via vacuolar K^+ concentration (Beilby and Casanova 2014). In general, four groups of charophytes can be distinguished in relation to habitat salinity (as summarized by Martin et al. 2003 and García and Chivas 2006): freshwater species (e.g. many *Nitella* species), oligohaline halotolerant species (e.g. *Nitellopsis obtusa* (Desv.) J. Groves 1919, up to 5 psu), mesohaline species (e.g. *Chara canescens* Loisel. 1810, *Chara aspera* Willd. 1809, up to 15 psu) and euryhaline species (e.g. *Lamprothamnium* species, 20-40 psu, up to 70 psu).

Most charophytes seem to tolerate variable water temperatures. Their tolerance can be species-specific (Rojo et al. 2017), and this is largely reflected in geographic distribution (Khan 1991). Temperature tolerance/requirement is a crucial factor for distribution along changing altitudes (e.g. Haas 1994; Calero et al. 2017). Most species prefer warm waters, hence diversity and abundance decreases at high altitudes and high latitudes. Nevertheless, there is a group of stenotopic species (e.g. *Tolypella canadensis* T. Sawa 1973, *Nitella opaca* (C. Agardh ex Bruzelius) C. Agardh 1824, *Nitella hookeri* A. Braun 1849, *Chara strigosa* A. Braun 1847), that prefer lower water temperatures (Krause 1997, Casanova et al. 2007). Temperature also seems to be very important for the growth and development of charophytes, affecting the maturation of gametangia (Calero et al. 2017) and having a role in breaking dormancy of oospores (Holzinger and Pichrtová 2016).

Although charophytes can be found on different types of substratum (peat, sand, clay and even rock) many species prefer flat-bottomed bathymetry and stable sediments

(Andrews et al. 1984; Sanderson et al. 2008). Few species are common in running waters (Krause 1997), and those that occur there are often found in back-waters, or slow-moving parts of the stream. Bathymetry is one of the factors affecting species diversity of charophytes (Pukacz et al. 2016b) as well as their spatial distribution (Pełechaty et al. 2004) due to the low strength of rhizoids. For this reason the larger charophytes are confined to areas without wave action. In contrast, there are some small charophytes whose well-developed rhizoids (e.g. *Chara aspera* or *Chara virgata* Kütz. 1834), facilitate their occurrence in very shallow, steep and high-wave-action sites.

There have been few studies on charophyte occurrence in relation to substratum type. Since charophytes lack the complex root and hollow stem systems of vascular macrophytes they cannot facilitate oxygen release into the rhizosphere (Matheson et al. 2005), and this could affect their capacity to penetrate and absorb nutrients from anoxic or toxic soils. Casanova (1994) found a relationship between different parent-rock types and the occurrence of some species (e.g. *Nitella arthroglochin* (Nordstedt) Casanova 2007 on granitic soils), but any relationship between charophyte growth and distribution and substratum type is largely unexplored. Where substratum has been studied, charophytes have been found to produce considerable amounts of nutrient-rich sediments which do not limit their growth (Kufel and Kufel 2002).

Nasty neighbours and fancy friends – interactions between charophytes and their biotic environment

Charophytes are not alone in aquatic environments, they contribute to food webs and habitat provision, they coexist, compete with and facilitate or hinder the existence of other organisms. In ancient times, charophytes dominated the submerged vegetation in shallow freshwater and probably many brackish water ecosystems. Since the angiosperms showed up on the “stage” around 200-250 million years ago (Morris et al. 2018), however, interactions with these “newcomers” have been one of the most important issues in the life of the phylogenetically far older (Domozych et al. 2016) charophytes.

Charophytes today occur mainly in mesotrophic ecosystems. Competition for light is assumed to restrict “bottom-dwelling” charophytes from turbid, eutrophic water where

angiosperms can form “canopies” along the water surface and thus are able to “escape” from low light availability in the water column (Blindow 1992).

Charophytes have been shown to produce (Wium-Andersen et al. 1982) and excrete (Blindow and Hootsmans 1991) toxic compounds which can potentially serve as allelopathic substances and reduce the densities of both phytoplankton and epiphyton (Pakdel et al. 2013). While this has been shown in the laboratory (Blindow and Hootsmans 1991; Mulderij et al. 2003; Pakdel et al. 2013), it is hard to quantify the importance of this mechanism in the natural ecosystem (Hilt and Gross 2008).

In oligotrophic to mesotrophic hardwater ecosystems, however, charophytes can form a dense and often winter-green vegetation. Efficient bicarbonate assimilation (van den Berg et al. 2002) as well as long-term immobilisation of nutrients by uptake, and also co-precipitation of phosphorus with carbonates (Kufel and Kufel 2002; Siong and Asaeda 2006) renders them superior competitors to angiosperms and facilitates low densities of phytoplankton (Blindow et al. 2014). Charophytes function as “key organisms” in such “*Chara*-lakes” (Samuelsson 1925) and exert a major impact on the whole trophic web. They offer food, and shelter from predation, for zooplankton, macroinvertebrates and fish larvae (Jones and Sayer 2003), though low densities of zooplankton are common in charophyte-dominated lakes possibly due to low food availability and / or high densities of smaller fish (Blindow et al. 2000; 2014). The role of charophytes as ‘ecosystem engineers’ can influence the abundance of invertebrate-eating as well as piscivorous fish, since these are favoured by high food availability and high water clarity (Hargeby et al. 1994; 2005; Schulze et al. 2006). Numbers of both breeding and resting waterfowl have been shown to follow changes of charophyte abundance and thus availability of both plant and invertebrate food in shallow lakes (Hargeby et al. 1994; Milberg et al. 2002).

By a number of feedback-mechanisms, charophytes can improve their own light availability and “stabilize” their dominance in shallow aquatic ecosystems: reduction of nutrient availability, mechanical reduction of wave action and thereby decreased sediment resuspension (van den Berg 1998a, b; Casanova et al. 2003) and possibly allelopathy are such mechanisms. These also impact on higher trophic levels such as increased predation efficiency of piscivorous fish and higher zooplankton densities, mechanisms that “cascade down” the food web and ultimately cause reduced phytoplankton densities (Scheffer et al. 1993). Charophyte-dominated lakes thus

belong to the first (Blindow et al. 1993; Scheffer et al. 1993) and most convincing (Capon et al. 2015) examples of ecosystems for which the existence of alternative stable states has been suggested, and are assumed to stabilize their environment more “reliably” than angiosperms (Blindow et al. 2014). While a positive impact on zooplankton is assumed to be the most important feedback mechanism in angiosperm-dominated lakes, charophytes are assumed to stabilize the clearwater state mainly by nutrient immobilization, reduced sediment resuspension and effects on the benthic foodweb (Figure 2). Recent research distinguishes among three stable states in freshwater lakes: a phytoplankton-dominated “turbid” state, a rather unstable “crashing” state dominated by submerged angiosperms, and a stable, “clear” state dominated by charophytes (Sayer et al. 2010).

While charophytes favour - and are favoured - by “friendly” organisms such as zooplankton, piscivorous fish and most plant-associated macroinvertebrates, herbivorous animals can harm charophytes and act as “nasty neighbours”. Grazing by fish, beetles, amphipods and other invertebrates is thought to have an important role in the distribution and abundance of grazing-sensitive/insensitive species (Proctor 1999). Grazing from waterfowl seems not to have an overall strong impact on charophytes (Rip et al. 2006) and only occasionally damages these macrophytes severely (Matuszak et al. 2012). Sediment-disturbing fish such as carp or bream, as well as crustaceans (e.g. *Lepiduris* spp), and especially invasive or stocked crayfish, can cause substantial declines in charophyte vegetation (Bakker et al. 2013; van der Wal et al. 2013). A strong impact has also been observed from invasive herbivorous fish (Jellyman et al. 2009).

To improve water quality and create better conditions for both bathing and fishing, submerged macrophytes have been planted in a number of shallow aquatic ecosystems (Bakker et al. 2013). Charophytes are regarded as especially suitable for this purpose because of their strong feed-back mechanisms, but also as their biomass often does not reach the water surface in contrast to “canopy-forming” angiosperms (Hilt et al. 2006). They can be planted as green biomass and / or by the import of sediment that contains charophyte oospores (Hilt et al. 2006; van de Weyer 2017).

Living at the edge – persisting periods of inconvenient conditions

There are some perennial species e.g. *Nitellopsis obtusa*, *Chara tomentosa, Chara australis* R.Brown 1810 and *Chara subspinosa* Rupr. 1846, that are able to withstand strong competition with embryophytes by features typical of K-selected species i.e. few, large offspring and a perennial, polycarpic life-history (Blindow et al. 2002; Luther 1951). Other charophytes, with features consistent with r-selected species (many, small offspring and an annual, monocarpic life-history), can be regarded as survival specialists, often being well adapted to variable and ephemeral habitats (Migula 1897). The production of numerous oospores (Figure 3), which can persist for decades or even centuries (Stobbe et al. 2014) within just a few weeks, allows them to continuously re-occupy extreme habitats like flood ponds, ephemeral wetlands or arctic springs, which offer favourable growth conditions irregularly or for short periods (Langangen 2000; Raabe 2009; Casanova and Porter 2013). The same holds true for other kinds of extremes e.g., extreme salinity. Unusual salinity conditions with respect to concentration, variability in time as well as ionic composition (e.g. Lambert 2013) offers niches where some charophyte species are superior competitors to embryophytes. This is also true for habitats with variable temperatures, either unusually high (Saber et al. 2017) or low (Langangen 2007). The clue for this amazing broad range of tolerances within a very small group of organisms might be their simple organisation, allowing for efficient growth in the short periods of favourable conditions, in combination with a diaspore of extreme persistence. They are often the first plants to colonize newly dug or cleared ponds and ditches, and some species are characteristic of ephemeral water bodies that dry up completely in the summer (Bicudo and Bueno, 2013; Casanova & Brock 1990; Casanova et al. 2003). However, in the long run, they are outcompeted by embryophytes as soon as nutrient levels and a certain stability of water level allow for the establishment of rooted embryophytes (e.g. Blindow 1992). In such systems charophytes are restricted to habitats were the relatively slow growing embryophytes are either hampered by mechanical disturbances (e.g. cattle grazing behind the reed belt or ice scraping (Idestam-Almqvist 2000; Blindow et al. 2016), or by water level variation (Becker 2011). Any serious disturbance of such systems e.g. drawdown of regulated lakes, creates an opportunity for charophytes to establish and to replenish the diaspore reservoir until being outcompeted again („permanent pioneers“, Krause and Walter 1985). In freshwater as well as coastal systems, the numbers of charophyte diaspores outnumber all other taxonomic groups by far, but the oospore

bank can also contain species which have not been detected at the respective sites for decades (Olsen 1944; Steinhardt and Selig 2007; Nowak et al. 2017).

Summary and knowledge gaps

From an ecologists' point of view the available data show that occurrence or absence of charophytes is not just a reflection of water properties such as nutrient availability or ion composition. Charophytes, like all organisms, have a complex niche structure with a multitude of potential limitations. Moreover, as an ancient, evolving group of organisms consisting of many cosmopolitan species, it is not surprising that niche structures are highly species-specific. There might be similarities within some groups with respect to preference ranges, but there is little in common with respect to "ecology of charophytes" at a family level (Doege et. al 2016; Schubert et al. 2017). The fact that many charophyte species dominate the macrophytobenthos of clear-water ecosystems makes them good bioindicators; however, they are not physiologically restricted to such conditions, they are just more competitive under low-nutrient-clear-water-conditions than angiosperms. But most, if not all of the indicator organisms in use can also be found under eutrophic turbid water conditions when competitors are missing. The reasons for reduced competition are manifold: unusual ionic composition (e.g. Krawczyk et al. 2016; Rybak et al. 2017), low-frequency mechanical disturbance (e.g. ice-scraping: Idestam-Almqvist 2000; Blindow et al. 2016); extreme osmotic regimes (e.g. Lambert 2013); irregular pond-bed drawdown (e.g. Lambert et al. 2013) just to name a few. All of them favour r-selected organisms, able to colonise fast and to resist even prolonged periods of harsh conditions by having resting stages that persist decades or longer in dormancy (Stobbe et al. 2014).

On the other hand not all of the species are such "pioneers". Several species develop dense vegetation in shallow lakes and brackish lagoons, where they are superior competitors due to a number of feedback mechanisms, which include both abiotic impacts and complex biological interactions (Blindow et al. 2014). This life form is equivalent to that of K-strategists and differs from the r-selected "pioneers", as some of these "competitors", such as *Nitellopsis obtusa* and *Chara tomentosa*, only produce low numbers of oospores and therefore have a limited dispersal ability.

It is when charophytes just do not "behave" as expected:

- when species such as *Chara hispida* L. 1753 s. auct. mult. and *C. aspera* “switch niches” and build up a dense, persistent vegetation in shallow lakes, as well as act as “pioneers” in nearby small water bodies (e.g. Blindow et al. 1993);
- when *Nitellopsis obtusa*, dioecious with low oospore production, becomes a “nuisance”, appearing as invasive plant in North America (Alix et al. 2017);
- when *Tolypella intricata* (Trentep. ex Roth) Leonh. 1863 “spontaneously” shows up in habitats that are “only briefly aquatic” (Moore 1986) such as mud trampled by lifestock or lorry tracks in a forest while several *Nitella*-species with rich oospore production “insist of being rare” and do not colonize any of the numerous apparently suitable habitats in their neighbourhood (Moore 1986; Blindow 2008);

then it becomes obvious that in addition to the ongoing work on taxonomic and evolutionary aspects of charophytes, ecological studies are likely to produce exciting insights into ecological theory (e.g. Capon et al. 2015) and management.

There is still a large gap in knowledge about growth, oospore production, germination and dispersal for example, as well as mechanisms facilitating persistence and (re)establishment of charophyte vegetation, which should be filled not only for scientific and management reasons, but also as this knowledge is badly needed to protect this ancient group of permanent pioneers and ecosystem engineers.

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Figure legends:

Figure 1

General morphology of a charophyte. Germination of the oospore results in the formation of a primary rhizoid and a protonema (also called “prochara”). The latter differentiates into a colourless basal cell between the primary rhizoid (directly inserted at the oospore) and the first bunch of secondary rhizoids, originating from the protonematal rhizoidal node. The primary internodal cell connects to the (only) protonematal axis node, the origin of the charophyte thallus. Drawing and oospore photograph: Anja Holzhausen; axis and branchlet node photographs: Andrzej Pukacz.

Figure 2.

Feedback-mechanisms stabilizing the clearwater states in lakes dominated by canopy-forming angiosperms (upper panel) and in lakes dominated by “bed-forming” charophytes (lower panel). The qualitative effect of each route in the diagram can be computed by multiplying the signs along the way. Dark areas and thick arrows indicate major feedback mechanisms. Light areas and thin arrows indicate feedback mechanisms of minor or unknown importance. Drawings after Scheffer et al. (1993) and Blindow et al. 2014, modified.

Figure 3.

Fundamental and realised niches of charophytes. Charophytes are able to grow from surface down to depths, where irradiance ultimately limits the existence of photoautotrophs (compensation depth). In absence of embryophytes, charophyte meadows may spread from compensation depth to the shoreline. However, under eutrophic conditions embryophytes are favoured, so charophyte meadows become squeezed between the irradiance limit for embryophytes and the compensation depth. For the rest of the littoral zone charophytes are restricted to a few niches where they grow underneath embryophytes (semiaquatic plant belt and floating plant belt) or where embryophytes cannot stand repeated mechanical disturbance by, e.g. grazing (semiaquatic belt). Drawing: H. Schubert; left and middle photographs: A. Pukacz; right photograph: S. Wesołowski.